

**STUDIES ON THE PHYTOPLANKTON
OF SOME LAKES CONNECTED WITH OR RECENTLY
ISOLATED FROM THE BALTIC**

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Aim of the Investigation

The province of Uppland, Central Sweden, offers conditions very suitable for regional limnological studies, including investigations on the phytoplankton. All lakes of the province are situated less than 80 m above the sea, and there are many examples of different types (WILLÉN 1954, map, p. 34*); Fig. 21, p. 50; p. 51 ff.). The landscape is intersected by shallow, wide rift valleys and has a coast line broken up into countless isles and islets. As a consequence, the post-glacial land uplift (50–60 cm per century) results in the continuous separation of new lakes along the coast of the Baltic. The present paper gives a summary

*) *Erratum*. "5 km" on the scale should be "25 km".

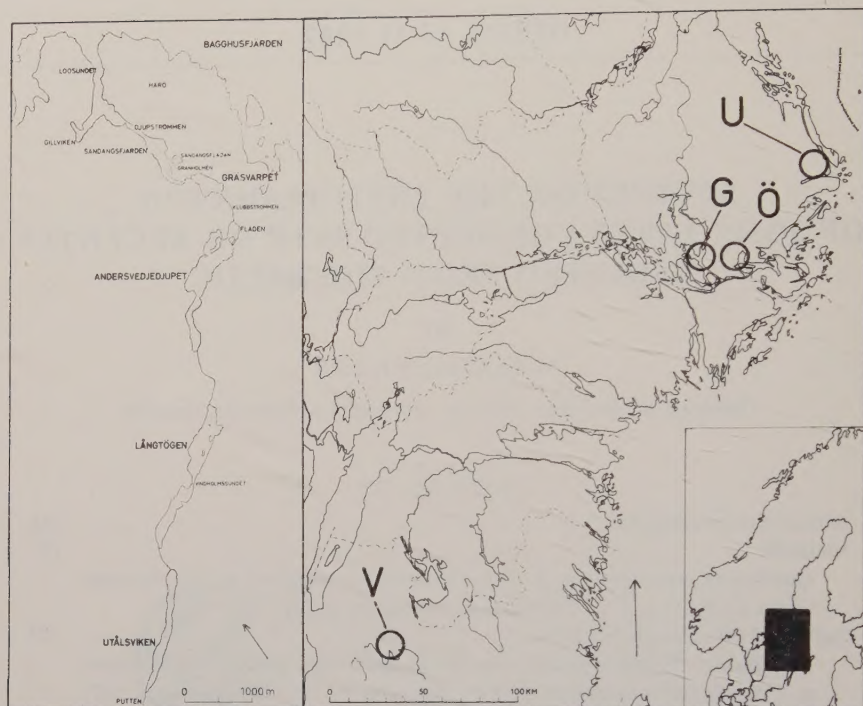


Fig. 1. Position of the investigated lakes. Left: the Utål Lake Chain. U the Utål Lake Chain; G Görvålän; Ö Ösbysjön; V Lake Södra Vixen.

of some investigations earlier published by the author (WILLÉN I–IV in the list of references), all dealing with the phytoplankton composition of lakes situated near the Baltic (Fig. 1) and at a level of at the most 7.3 m above sea level. All the lakes are situated in the south-eastern part of the province.

The Utål Lake Chain (WILLÉN IV), studied from 1953 to 1961, with a general quantitative investigation of the phytoplankton in 1955–1956, was chosen as an example of bodies of water forming a series of steps from the Baltic to a height of 1.4 m above sea level.

Görvålän (WILLÉN I) is a part of Lake Mälaren (0.3 m above sea level). From this “fjärd” (see WILLÉN IV, p. 13) drinking water for the northern suburbs of Stockholm is taken by the waterworks at Görvålän. A range of limnological investigations, including analyses of the standing crop of phytoplankton, was carried out from May 1955 to May 1956.

Ösbysjön (WILLÉN II and III), situated 7.3 m above sea level, was studied from several points of view (June 1957 to July 1958) to provide a thorough description of the lake before a planned alteration of the bottom sediments, higher plant vegetation etc., in order to make the lake more suitable for bathing.

Results of these investigations have so far been published in the following papers: FORSBERG (1960) on the aquatic macrovegetation, FRIES (1962) on pollen and sediment analyses and PEJLER (1961) on the zooplankton.

This selection of lakes does not give a complete picture of the various types of lakes and their phytoplankton. The aim of the present study is only to give an example of a developmental sequence, ranging from the brackish water fjärds via the flada stage to various kinds of freshwater lakes, although other types of such sequences may occur.

Comparisons can also be made with another lake, Södra Vixen, province of Småland, South Sweden (WILLÉN 1961), which was studied May 1955 to November 1957. This lake is of a quite different type. It is a clear-water lake, situated ca. 215 m above sea level, with a moderate phytoplankton development.

Methods

Qualitative investigations

Whenever possible, qualitative investigations of phytoplankton were performed on living material. The samples were collected by means of a plankton net (Müller gauze no. 25) and fixed in formalin and/or Lugol-Rodhe solution¹).

In addition plankton was concentrated by centrifuging water samples from different depths. Since in most cases both qualitative and quantitative analyses were performed there was often insufficient time to identify all organisms, and so certain small flagellates may often have been neglected. As pointed out in connection with the published lists of species, the lists are not quite complete: it would certainly be possible to add several species by repeated analyses of the samples. – Some taxonomic notes are given in WILLÉN 1962.

Quantitative sampling

As a rule, the samples for quantitative analysis were collected with a Ruttner water sampler. To 100 ml of the sample two drops of Lugol-Rodhe solution were added. Usually the samples were analysed within a few weeks; however, samples kept in darkness have proved fit for analysis even after four years. It is necessary to keep the samples under control and to add a few drops of the preservative if the yellow-brownish colour is fading.

All samples have been stored in glass bottles. During the field work, however,

¹) 10 g I₂ + 20 g KI + 200 g aqua dest. + 20 g glacial acetic acid (cf. RODHE, VOLLENWEIDER & NAUWERCK 1958, p. 302). The addition of acetic acid (or sodium acetate, according to UTERMÖHL 1958, p. 10) gives a better preservation of the organisms. Flagellates provided with calcareous loricae or shells did not occur to a significant extent in the relevant bodies of water.

it was more practical to use bottles of polyethylene. Polyethylene bottles are stained by the iodine; however, in experiments it has been shown that the organisms do not adhere to the inside of the bottles to any marked extent.

As a rule, samples were collected every 14 days, from the breaking up of the ice to late autumn, and once a month during the winter (Görvåln and Ösbysjön). In the investigation of the Utål Lake Chain, 1955–1956, samples were collected at somewhat greater intervals. Moreover, immediately after the breaking up of the ice, the sampling was intensified in Görvåln (e. g., samples were taken on 8, 11, 14, 18 and 28/V, 1956). The routine programme was often supplemented by additional samplings. VERDUIN (1951, p. 11) recommends “a sampling frequency at about 3-days intervals” during the phase of most active growth of a plankton community.

In Ösbysjön (WILLÉN III, p. 199–202) the developmental sequence was studied through sampling every day for a period of six days in July 1958. During this “quiet” period, however, the plankton development was harmonic with relatively low total volume values.

From the Utål Lake Chain (and Lake S. Vixen) samples were generally only collected from a depth of 0.3–0.5 m. In Görvåln, Sandängsfjärden (belonging to the brackish water area of the Utål Chain) and Ösbysjön the vertical distribution of phytoplankton was studied in more detail with sampling at 5 or 6 specified depths.

The horizontal distribution within a lake has only been studied in Ösbysjön (WILLÉN III, pp. 196–199), where no noteworthy differences were recorded.

Quantitative analysis

The quantitative analyses were performed according to the Utermöhl technique (UTERMÖHL 1931a, p. 567 ff.; 1931 b, p. 643 ff.; 1936, p. 1879 ff.; 1958; cf. also 1925; 1927, p. 464 ff.).

For sedimentation, counting-chambers of “Verbundkammer” type were used (UTERMÖHL 1958, p. 19 ff.). They consist of two parts: a flat bottom chamber, “Plattenkammer”, and a cylinder. This latter may be of various heights (and volume). After ca. 24 hours, when all organisms have settled on the bottom of the flat chamber, the cylinder is pushed off, and the flat chamber transferred to the microscope for counting. A special filling-chamber has not been used. In fact, the organisms settle within a considerably shorter time than 24 hours (cf. LUND, KIPLING & LE CREN 1958, p. 150), but it is convenient to fill the sedimentation tubes one day and to perform the analyses the following day.

Counting-chambers containing 1, 10, 25 and 50 ml were used. The 1 ml chamber was used for analysing organisms occurring in large numbers; in this

case, the whole bottom area of the chamber was examined. For counting organisms occurring in small and moderate numbers volumes of 5, 10, 25 or 50 ml were used.

The organisms were counted with an inverted plankton microscope (Zeiss). In 1955–1956 the microscope was without phase contrast but later a microscope with this equipment was used. With phase contrast it is considerably easier to count and identify delicate organisms such as *Attheya*, *Bicosoeca*, *Dinobryon*, *Rhizosolenia* and many other small flagellates. Both *flagella*, *loricae* and collars are easy to study. Also the count of very small organisms (ultraplankton or μ -plankton) is facilitated. They have been counted in the ordinary counting-chambers using oil immersion (Neofluar 100/1.30 Oel, ocular 8 $\times$); the method (RODHE 1955, p. 118) used when analysing the samples from Görväln (WILLÉN I, p. 243), i. e. counting the ultraplankton by means of a water immersion objective on an ordinary microscope to which the counting-chamber was transferred, does not give as good results as those obtained with the inverted microscope by means of oil immersion and phase contrast. – With the mentioned exception (μ -plankton from Görväln) all analyses have been performed in the same manner.

In counting it is a waste of time to use a higher magnification than that by which the organisms are easily identified. Most taxa may be counted at a low magnification, while a higher magnification must be used for nannoplankton and the highest possible for ultraplankton. When counting the usually very frequent nannoplankton and ultraplankton it is not necessary to examine more than a small part of the bottom area of the chamber. Using an ocular crossed by three lines, one of which is fixed with the other two perpendicular to it and adjustable to a definite distance from each other, and with a movable stage on the microscope, a fixed area of the flat chamber can be analysed. If the sedimentation has been uniform, it is then possible to calculate the number of organisms per millilitre or litre. If, on the other hand, the organisms are crowded along the periphery or gathered in a part of the chamber, an analysis is of no value and it is necessary to make a new preparation.

A complete analysis of a sample involves the examination of at least two counting chambers: 1 ml and 10, 25 or 50 ml. Most of my analyses are complete; in some cases, however, it may be permissible to confine the analysis to a comparatively small number of taxa and to perform only a “1 ml analysis”. As a rule, a lake may be characterized quantitatively by less than 20 different species, as pointed out by NAUWERCK (1955, see also WILLÉN 1960, p. 139, Fig. 8). DAVIS (1958, p. 20) enumerates 40 important taxa, which he has counted and included in his volume calculations. – A simplified analysis saves a lot of time and is often to be recommended for investigations of a practical nature. The Utermöhl technique has often been rejected, being regarded too time-

consuming, "though this is probably one of the most accurate methods known" (SMALL 1961, p. 344).

As a rule, the most frequently occurring taxa were counted in appreciably more than 100 units per chamber, hence giving a good statistical basis (UTERMÖHL *op.c.*, p. 30). Several controls of the counts have been performed, both by comparing different bottom strips from the same counting-chamber and by comparing different chambers filled with water from the same sampling-bottle, but no statistical tests have been performed. For reliability of single observations of phytoplankton and statistical tests see UTERMÖHL (*op.c.*, p. 29 ff.), LUND, KIPLING & LE CREN (*op.c.*, p. 143 ff.), HASLE (1954, p. 125 ff.), BALLANTINE (1953, p. 129 ff.), JAVORNICKY (1958, p. 283 ff.) etc. In the two latter papers the results of different methods have been compared.

The Utermöhl technique used for marine plankton investigations was discussed by STEEMANN NIELSEN (1933, p. 201 ff.), who compared this method with "counts made after centrifuging corresponding samples" (*op. c.*, p. 209). Different centrifuging methods were earlier in common use for quantitative analyses both of marine and freshwater plankton (see e.g. PASCHER 1912, p. 93 ff.). STEEMANN NIELSEN showed that the Utermöhl technique gives a considerably better result than the earlier methods.

BRAARUD (1958, p. 17 ff.) has also compared different methods for quantitative phytoplankton studies: net methods, centrifugation, filtration, sedimentation, direct counts and culture methods. "The sedimentation method with the use of inverted microscope may be regarded as the most satisfactory standard method for obtaining quantitative records of the phytoplankton, except for the smallest groups" (*op.c.*, p. 18). As pointed out above (p. 173), it is no problem to perform a satisfactory analysis with the inverted microscope of even ultraplankton by using high magnification (oil immersion) and phase contrast.

Obvious disadvantages of the method, pointed out e. g. by BRAARUD (*op. c.*), are that only fixed samples can be analysed and that the organisms are lying in "closed" chambers, both conditions rendering an exact identification more difficult. It is also necessary to use a relatively expensive microscope with special equipment. LUND (1951, p. 390 ff.) has described a simplified method for counting plankton algae.

Surveys of quantitative methods have been given in several other papers, e. g. by GESSNER (1959, p. 487 ff.), KREY (1950, p. 58), LITTLEFORD, NEWCOMBE & SHEPHERD (1940, p. 309 ff.), LUND & TALLING (1957, p. 514 ff.) etc.

The results of a quantitative investigation might be given only as numbers of cells, colonies or trichomes of the different taxa but this would be of limited interest. The aim of a quantitative investigation is to find the relative importance of the organisms, and this is best expressed as the total volume (or weight). From the total volume values obtained it is possible to make adequate com-

parisons between different values from the same lake, or values from different bodies of water. It is also possible to compare different methods to estimate the standing crop or the productivity of the water.

The approximate volume of most organisms is relatively simple to calculate from the formulas of the cube, cylinder, sphere, etc. The volume of cells of roundish cylindric shape are calculated according to the formula given by FETZMANN (1956, p. 732). Gelatinous envelopes and spines of the organisms have not been included (cf. LOHMANN 1908, p. 197) nor the loricas of *Bicosoeca*, *Dinobryon* etc.

The length of trichomes (*Anabaena*, *Aphanizomenon*, *Oscillatoria*, *Melosira*, etc.) has been measured, and the sum is expressed in cm or m per litre. When very large numbers occurred, e. g. of *Aphanizomenon* or *Melosira*, the different trichomes have been grouped into classes with average lengths of 100, 200, 300 and 400 μ etc.; otherwise, each single trichome was measured with the use of an ocular micrometer. For calculating their volume the trichomes were regarded as cylinders.

Plankton algae occurring as coenobia (*Coelastrum*, *Pediastrum*, *Scenedesmus*, etc.) were counted as 2-, 4-, 8-, 16-, 32- or 64 cells coenobia. The number of cells of colonial algae (*Dictyosphaerium*, *Gloeococcus*, *Kirchneriella*, *Selenastrum*, etc.) can often be counted exactly; in other cases, an estimate of the number of cells was made. In the diatom genera *Asterionella*, *Chaetoceros*, *Diatoma* and *Tabellaria* the number of cells, not colonies was counted. Species of the genera *Staurostrum* – always in moderate quantities in these lakes – were classed in different groups of size and the average volumes were calculated.

Colonies with a large number of cells (*Aphanocapsa*, *Microcystis* etc.) present considerable difficulties in volume calculation. In small and loose colonies it is possible to count the different cells; in dense colonies this is impossible. These colonies were measured and “transformed” to compact cubes or spheres of which the volumes were calculated.

Volume estimation inevitably involves some uncertainty. Measurements of 15–50 individuals of the same species were usually performed; however, it was impossible to check the volume of all species in every sample. Special attention was always paid to species of very varying size; e. g. species of *Anabaena*, *Oscillatoria*, *Chlamydomonas*, *Cyclotella*, *Melosira*, *Stephanodiscus*, *Gymnodinium* etc. (cf. e. g. HINTZ 1955, p. 271 ff., who has studied the variations in populations and cell dimensions).

For the method of volume calculations reference can also be made to NYGAARD (1949, p. 5) and JÄRNEFELT (1956, p. 2–5). The latter author analysed samples fixed in formalin or sublimate: then difficulties arise especially with the cyanophytes which do not precipitate on the bottom of the counting-chamber (cf. also HALME & MÖLDER 1958, p. 9).

Volume values for different organisms have previously been given by e. g.

LOHMANN (1908, p. 199), FETZMANN (op. c., p. 732 ff.), GISTL (1926, p. 480 ff., for desmids), GRIM (1939, p. 196), HINTZ (op. c., p. 275), NAUWERCK (in prep.), VERDUIN (1952, p. 164), etc.

The total volumes are expressed in $10^6 \mu^3/l$ (nearly equal to $\mu g/l$ or mg/m^3). FETZMANN (op. c., p. 732) gave the volume figures in "Kubikdekami" = $1,000 \mu^3$; DAVIS (op. c., p. 17) expressed volumes in cubic decimillimetres, $1 \text{ dmm}^3 = 10^6 \mu^3$.

Total volume values have been published by several authors. LACKEY (1941, p. 322) has calculated the average volumes of more than 400 species occurring in Scioto River in the same manner as described above and expressed "the population figures in parts per million by volume". About the method of calculation he writes (l. c.) "To those who find a large chance for error in such treatment, we can only reply that we do not know a better way of comparing the relationships between, say 5,000 *Chrysococcus refesceus* (sic!) and 2 *Euglena viridis* per ml". DAVIS (op. c., p. 17) also pointed out the errors inherent in the method which he used in his investigations in the western Lake Erie region. "The volumes given should be considered as approximations only, but it is felt that they are preferable (until more precise methods are devised) to no measurements at all".

The dividing line between net plankton and nanoplankton (cf. LOHMANN 1909, p. 234; 1911, pp. 1,3) has been set at 60μ in any one dimension (cf. NAUMANN 1931, p. 614). It is a conventional value: no large differences of the total volume of plankton would appear if 50 or 70μ were chosen.

Following RODHE (1955, p. 118) the term " μ -algae" was used for minute species ($< 5\mu$) of *Chlorella*, *Coccomyxa*, *Stichococcus* etc. in WILLÉN I, p. 271; II, p. 52. However, the terms "ultraplankton" *sensu* NAUMANN (op. c., pp. 440, 613-614) and UTERMÖHL (1931 a, p. 580, 1936, p. 1880), μ -plankton (see e. g. LUND & TALLING op. c., p. 535) or possibly " μ -cells" *sensu* DAVIS (op. c., p. 22) may be preferable, because of the fact that a large number of bacteriophytes will often be included in the counts of these organisms (cf. WILLÉN I. c.).

Graphical presentation

For the major chemical constituents (K, Na, Ca, Mg, SO_4 , Cl and HCO_3) the equivalent percentage diagram according to MAUCHA (1932) has been used (see WILLÉN IV, p. 34). This type of diagram is also applicable to the percentage distribution of algal groups (HORTOBAGYI 1957, p. 57 ff.). A circle divided into eight sectors was used by HORTOBAGYI (l. c.), one with twelve sectors by JÄRNEFELT (1952, p. 4). The groups illustrated in the diagram can be chosen according to their prevalence in the investigated lakes.

In the present investigation the 8-sectored circle has been used and the

percentage values of the total phytoplankton volume are illustrated. The following seven groups are shown in all diagrams: *Cyanophyta* (CY), *Euchlorophyceae* (CHL), *Desmidiaceae* (DE), *Chrysophyceae* (CHR), *Diatomeae* (DI), *Cryptophyceae* (PY) and *Peridineae* (PE). The eighth sector is thus open for "other groups". Sometimes one group e. g. *Euglenophyta* or *Heterokontae*, is common in summer and another in winter, e. g. *Bacteriophyta*. This is exemplified by the investigation of Ösbysjön (WILLÉN II, p. 65).

To illustrate the relation between a smaller number of groups the circle diagram has been used (WILLÉN 1960, p. 141, IV, p. 91). Such diagrams often require a number of symbols in order to be easily understood (see e. g. SZEMES 1959, p. 253).

The vertical distribution of phytoplankton is shown by spherical curves ("Kugelkurven"), in which all values indicate volumes per litre (see e. g. WILLÉN II, p. 40). The diameter of the cylinder is proportional to the cube root of the volume value (see LOHMANN 1908, p. 193; RUTTNER 1914, p. 277; 1938, p. 174; 1952, p. 92).

To illustrate the seasonal and vertical distribution of phytoplankton (percentage values or total volume values) three-dimensional diagrams or "wing-diagrams" have been used (see WILLÉN II, p. 46 ff.). This type of diagram has previously been published by JAAG (1949, p. 194; etc.). Of course, wing-diagrams may also be used to illustrate physico-chemical conditions (WILLÉN op. c., p. 39) as an alternative to the depth-time diagrams (see WILLÉN I, p. 246).

Survey of the investigated lakes

The Baltic: Bagghusfjärden and Sandängsfjärden

No physico-chemical or planktic analyses from the open Baltic Sea have been made. Bagghusfjärden and Sandängsfjärden (see map in WILLÉN IV, p. 12) are both situated inside the belt of skerries; the conditions of Bagghusfjärden (at Harö), however, are in general representative of the conditions prevailing in the Baltic. Some physico-chemical data have been given in WILLÉN IV, p. 24 ff.

At Harö (salinity 3.9–6.0 ‰) low phytoplankton volumes were recorded throughout the year (Fig. 3). Only in spring was an increased development of diatoms (*Chaetoceros*, *Diatoma*, *Skeletonema*, *Thalassiosira*, etc.) and dinoflagellates (*Gonyaulax*, etc.) observed. The total volume values ranged between $150 \cdot 10^6$ and $2,500 \cdot 10^6 \mu^3/l$ (1955–1956); the values from the ice period were even lower.

The number of species was also small (WILLÉN IV, Fig. 44, p. 137). Some taxa were specific for the brackish water and were recorded only in this part of the investigated area or sporadically in the flada area (see below, p. 190) to which

they were brought by inflowing brackish water. Among these taxa the following may be mentioned: *Nodularia spumigena*, *Dinobryon petiolatum*, *Chaetoceros* spp., *Skeletonema costatum*, *Thalassiosira baltica* and *Gonyaulax catenata*.

From Bagghusfjärden a narrow fjärd-system stretches inwards via Loösundet and the narrow channel of Djupströmmen to a somewhat larger fjärd, Sandängsfjärden. While the influence of freshwater was very unimportant at Harö, it became much more marked in the innermost parts of the system. Sandängsfjärden was studied in more detail (WILLÉN IV, p. 119 ff.) and here different zones could be distinguished characterized by very different salinities and phytoplankton populations. Throughout the year it was possible to find both freshwater and brackish water organisms and, as a rule, also specific populations adapted to the anaerobic conditions prevailing at a depth of 4–6 m.

Gräsvarpet

This lake belongs to the Utål Lake Chain (WILLÉN IV) together with the fjärd-system described above and the lakes Andersvedjedjupet, Långtögen and Utålsviken, which will be discussed in the following. Gräsvarpet normally contains freshwater but it is influenced by influxes of brackish water at times of high-water in the Baltic. As no tide of any importance is present in the Baltic the sporadic states of high-water are caused mainly by changes in weather conditions. The fluctuating chemical conditions caused great and sudden changes of the phytoplankton composition of Gräsvarpet.

In total, a large number of species occurred in the lake. These were mainly freshwater species, about the same taxa as those recorded in Andersvedjedjupet which flows in a short stream into Gräsvarpet. The influxes of brackish water brought some brackish water organisms into the lake. They were never observed for long periods. Gräsvarpet is a shallow lake (about 2 m deep) and there was never any lasting vertical stratification appearing as a result of the interchanges of freshwater and brackish water.

Gräsvarpet as well as Andersvedjedjupet have been referred to the flada stage (WILLÉN IV, p. 18). As mentioned above, this stage of isolation is characterized not only by large fluctuations in the level of the water, in physico-chemical conditions etc., because of the intermittent pulses of brackish water, but also by very large total volumes of phytoplankton, a mass development of some taxa and the occurrence of specific flada ("lagoon") diatoms.

The water temperatures become relatively high early in summer in Gräsvarpet (WILLÉN IV, p. 26) because of the shallowness of the lake, a condition which contributes to the development of large populations of cyanophytes and chlorophytes as early as June. During the period from May to mid-July a freshwater phase usually prevailed. The total volumes of phytoplankton re-

corded during this period were always very high (e. g., ca. $12,500 \cdot 10^6 \mu^3/l$ on 29/VI 1955). During July, however, there were influxes of brackish water, with a destructive influence on the existing populations (WILLÉN IV, Figs. 19, 20, 26).

In the flada stage environmental conditions were apparently very suitable for some species and these developed in enormous quantities. This occurred for the genera *Anabaena*, *Aphanizomenon*, *Oscillatoria* (*O. limnetica*), *Pseudanabaena* (*P. catenata*) and several diatoms, e. g. *Asterionella formosa*, *Diatoma elongatum*, *Melosira*, *Stephanodiscus* and *Synedra* spp.

The occurrence of some bottom and epiphytic diatom taxa (*Campylodiscus clypeus*, *Nitzschia scalaris*, etc.) is also a characteristic feature of the flada stage (WILLÉN IV, p. 142). In quaternary geological and limno-developmental studies the flada or *clypeus* stage is an important level of the sediments indicating the time of isolation from a brackish water stage. It is noteworthy that planktic diatoms (*Asterionella*, *Chaetoceros*, *Diatoma*, etc.) apparently very rarely occur in the sediments; studies restricted to quaternary deposits seem to give no complete picture of the flada organisms.

Andersvedjedjupet

The lake has been isolated from the Baltic during the last century but at the present time it is subject to small and sporadic influxes of brackish water at time of extreme high-water in the Baltic. These influxes never were observed to be so destructive to the phytoplankton (WILLÉN IV, p. 68) as those recorded in Gräsvarpet. Andersvedjedjupet was also characterized by very large total volumes of phytoplankton (Fig. 3). The developmental sequence, however, was here more gradual and the largest standing crops were recorded during late summer (July to September), with cyanophytes and diatoms predominating by volume.

Among the lakes of the Utål Chain, the largest number of taxa was recorded from Andersvedjedjupet. Besides cyanophytes and chrysophytes (diatoms included), in particular the chlorophytes apparently found favourable conditions in the lake (WILLÉN IV, Fig. 44). The *clypeus* flora also appeared in this lake. *Vaucheria* cf. *dichotoma* was observed in large yellow-brownish dead carpets on the bottom.

Görvåln

This bay of Lake Mälaren, 0.3 m above sea level, normally contains freshwater. The connections between the Baltic ("Saltsjön") and Lake Mälaren are regulated by locks; however, sporadic influxes of brackish water may occur (MELIN 1930, p. 256 ff.). The consequence of an influx at the end of 1955 was

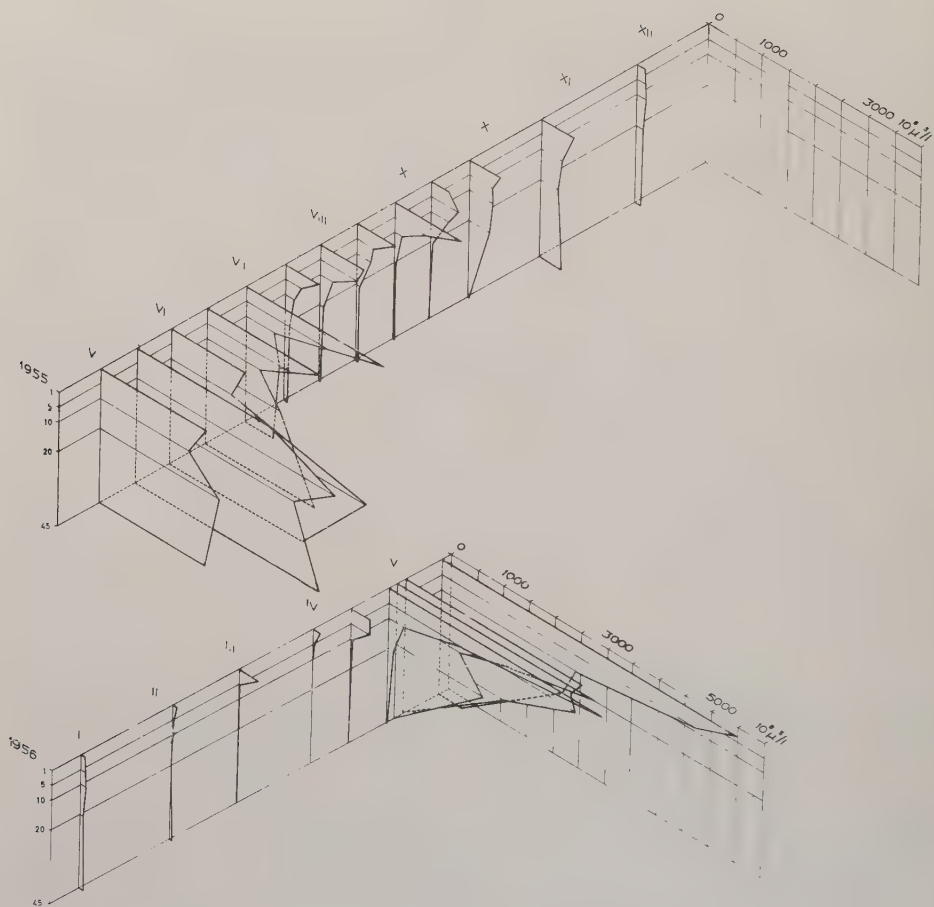


Fig. 2. Distribution of the total phytoplankton volumes in Görväln, 1955–1956.

studied in the investigation performed from May 1955 to May 1956 (WILLÉN I, p. 241 ff. ¹), 1960 p. 133 ff.). – Among the investigated lakes described in this paper, Görväln is the deepest (ca. 53 m); none of the other lakes is subjected to regulation of the water level.

The composition of phytoplankton was characterized by an immense development of diatoms (*Melosira islandica* ssp. *helvetica*, *Stephanodiscus* spp., etc.) in spring, and, to some extent, also in autumn; of pyrrophytes (cryptomonads) during July; and of cyanophytes (*Aphanizomenon flos-aquae*, etc.) in

¹) Errata. In WILLÉN I, Table 4, p. 265: *Peridineae* on 31/V 1955: 960.0 should be 96.0; *Cyanophyta* and *Chlorophyta* on 19/IX 1955: 46.3 and 4.3, respectively, should be 250.0 and 23.0, respectively; the total volume value (540.0) is correct. Table 5, p. 266: *Chrysophyceae* on 6/VI 1955: 33.8 should be 330.8.

late summer (WILLÉN I, Fig. 10, p. 267). In the middle of May 1955 *Synura petersenii* was also observed in large quantities. This species as well as *Thalassiosira baltica*, recorded in small quantities every year, apparently develops large populations at intervals of some years (personal communication by Mr. Å. SIKSTRÖM, Norsborg waterworks).

The total volumes of phytoplankton were high only in spring and early summer (diatoms and some chrysophytes). A picture of the distribution at different levels is given in a wing diagram, Fig. 2. From this diagram, from the spherical curves previously published (WILLÉN I, pp. 249–251) and from the given physico-chemical data (l. c., p. 245 ff.), it is evident that the influx of brackish water into Görvälän in 1955 caused a limitation of the vernal circulation in 1956. At the end of the summer 1956 somewhat raised values of the specific conductivity were still recorded at deeper levels.

Even if the total volume values were about the same during May both in 1955 and 1956, the diatoms apparently were stimulated to an increased development in 1956. Especially, the development of the genera *Asterionella*, *Diatoma*, *Melosira* and *Stephanodiscus* was increased in 1956 (except at deep levels). To draw any definite conclusions from a study of the spring outburst in only two years is not possible, but, as mentioned above, a similar tendency toward increased algal development was observed in the flada area of the Utäl Lake Chain. No specific brackish water organisms were observed in Görvälän, as the brackish water which had flowed into the deeper parts was very diluted. On other occasions, diatoms from the Baltic have been reported from Lake Mälaren by several authors (CLEVE-EULER 1912, FLORIN 1957, p. 93 ff., THOMASSON 1949, p. 56 ff.). *Chaetoceros muelleri* Lemm. and *Ch. wighami* Brightw. were reported by THOMASSON (op. c., p. 61); the latter species was also observed by HUSS & SONDÉN (1920, p. 7).

Långtögen

In the Utäl Lake Chain two genuine freshwater lakes are included, Långtögen and Utälsviken, situated 1.3 and 1.4 m above sea level, respectively. In Långtögen no features characterizing the flada stage apparently remained. The total volumes of phytoplankton were considerably lower (WILLÉN IV, Fig. 19), the peak values were caused by quite other taxa (e. g., *Uroglena americana*, *Stephanodiscus astraea*) and the specific *clypeus* flora was not observed in the living state. The number of taxa was considerably smaller than that recorded in the flada stage; the chlorophyte and diatom genera, in particular, were less numerous. *Coelastrum microporum*, *Volvox aureus*, *Mallomonas fastigata*, *Uroglena americana* and *Trachelomonas* spp. may be mentioned as examples of species characteristic of the lake.

Utålsviken

The last link of the Utål Lake Chain, Utålsviken, has a definite pond character. The lake is long and narrow, it is partly overgrown by higher plant vegetation and it has a somewhat higher specific conductivity than Långtögen (WILLÉN IV, p. 28). The total volume values of phytoplankton ($680 \cdot 10^6 - 3,400 \cdot 10^6 \mu^3/l$) were about the same as those recorded from Långtögen ($630 \cdot 10^6 - 2,700 \cdot 10^6 \mu^3/l$). Cyanophyte and diatom genera were of subordinate importance, while chrysophytes (*Dinobryon* spp., etc.) and dinoflagellates (*Ceratium*, *Peridinium*, etc.) predominated.

Ösbysjön

This small lake may definitely be characterized as a pond lake (WILLÉN III, p. 219). It is situated ca. 7.3 m above sea level; no lakes situated at heights between 1.4 m (Utålsviken) and 7.3 m have been studied in detail.

In summer the genus *Dinobryon* predominated in the lake together with some other chrysophytes. Cyanophytes, desmids and diatoms played a subordinate rôle throughout the year. In winter anaerobic conditions prevailed almost throughout the whole lake (WILLÉN II, pp. 42–44) and specific mud organisms adapted to these conditions appeared. These were bacteriophytes (*Chlorochromatium*, *Hyalosoris*, *Rhodotheca*, *Sarcina*, etc.), cyanophytes (*Oscillatoria*, etc.), euglenophytes (*Astasia*, *Menoidium*, etc.), cryptophytes and dinoflagellates (*Glenodinium*, etc.), all in immense quantity. In fact, the highest total volume values (ca. $3,000 \cdot 10^6 \mu^3/l$) were recorded when the lake was ice-covered, even if high volume values also were reached in summer (ca. $2,300 \cdot 10^6 \mu^3/l$; mainly caused by *Dinobryon* spp.).

About the same mud organisms as those occurring in winter were also recorded in summer near the bottom of the lake, when there were low oxygen concentrations.

Seasonal and vertical distribution of phytoplankton*Seasonal development*

By means of quantitative phytoplankton investigations throughout a year a relatively good picture is gained of the species occurring and of their seasonal variation. In general, plankton algae are to be referred to the group of "Ephemerals" (TRANSEAU 1916, p. 125): most of them appear during a short period of the year, demanding rather specific conditions of temperature, light intensity and nutrient substances. The developmental sequence may differ considerably from one year to another, but, as a rule, similar features of the seasonal develop-

ment may be distinguished every year. There is naturally a seasonal variation in the quantitative development at different latitudes governed by the lengths of the "biological seasons" (see BOGOROV 1958, pp. 148–149).

Fig. 3 shows the total volume values obtained from the investigations of Harö, Gräsvarpet, Andersvedjedjupet, Görvälän and Lake Södra Vixen (WILLÉN 1961) in 1955–1956 and of Ösbysjön in 1957–1958. The values from Långtögen and Utålsviken (see WILLÉN IV, Fig. 45, p. 138) showed no remarkable features and have been excluded.

Those algae which develop very large populations in connection with the spring outburst were often already observed before the time of melting of the ice (e. g. some diatom species in Görvälän, WILLÉN I, Fig. 4c, p. 251). In most lakes, the highest total volumes were recorded within a period lasting for three or four weeks from immediately after the breaking up of the ice. The diatoms were usually definitely predominant during this period, but consisted only of a small number of taxa. At Harö, *Chaetoceros* spp., *Diatoma elongatum* and *Skeletonema costatum* predominated; in Sandängsfjärden and Gräsvarpet, *Diatoma elongatum*; in Andersvedjedjupet, *Asterionella formosa*, *Diatoma elongatum* and *Melosira* spp.; in Görvälän, *Melosira islandica* ssp. *helvetica* and *Stephanodiscus* spp.; in Lake S. Vixen, *Asterionella formosa*, *Stephanodiscus* spp. and *Tabellaria fenestrata*.

Among the nannoplanktic diatoms, *Stephanodiscus hantzschii* (including var. *pusillus*) was often found in immense quantities; in particular, it was common in Gräsvarpet, Andersvedjedjupet (and Fladen) and in Görvälän.

However, in some lakes the total volumes were moderate in spring and groups other than *Diatomeae* played the principal rôle. Such conditions apparently prevail in Långtögen, Utålsviken and Ösbysjön. In all these lakes the peak volume values were observed at other seasons. In Långtögen and Utålsviken, the *Chrysophyceae* predominated in spring. The group consisted of several genera, *Chrysococcus*, *Dinobryon*, *Erkenia*, *Mallomonas*, *Synura*, *Uroglena* and other small flagellates. Some of these genera, however, showed their definite maxima somewhat later (*Mallomonas*, *Dinobryon*, *Uroglena*). Together with these chrysophyte genera, cryptomonads, rhodomonads and a few diatom genera (e. g. *Asterionella*, *Synedra* and *Tabellaria*) etc. were also recorded.

While a more or less marked increase of the total volumes was observed in all other lakes, the developmental sequence in Ösbysjön was quite different. After very high total volume values in winter the phytoplankton volume decreased definitely at and after the time of the breaking up of the ice. Here the *Cryptophyceae*, *Chrysophyceae* and *Cyanophyta* predominated, while *Diatomeae* played quite a subordinate rôle. Within a month, however, the chrysophytes had increased to absolute dominance and this group alone (mainly some *Dinobryon* spp.) characterized the lake during the period when it was free from ice.

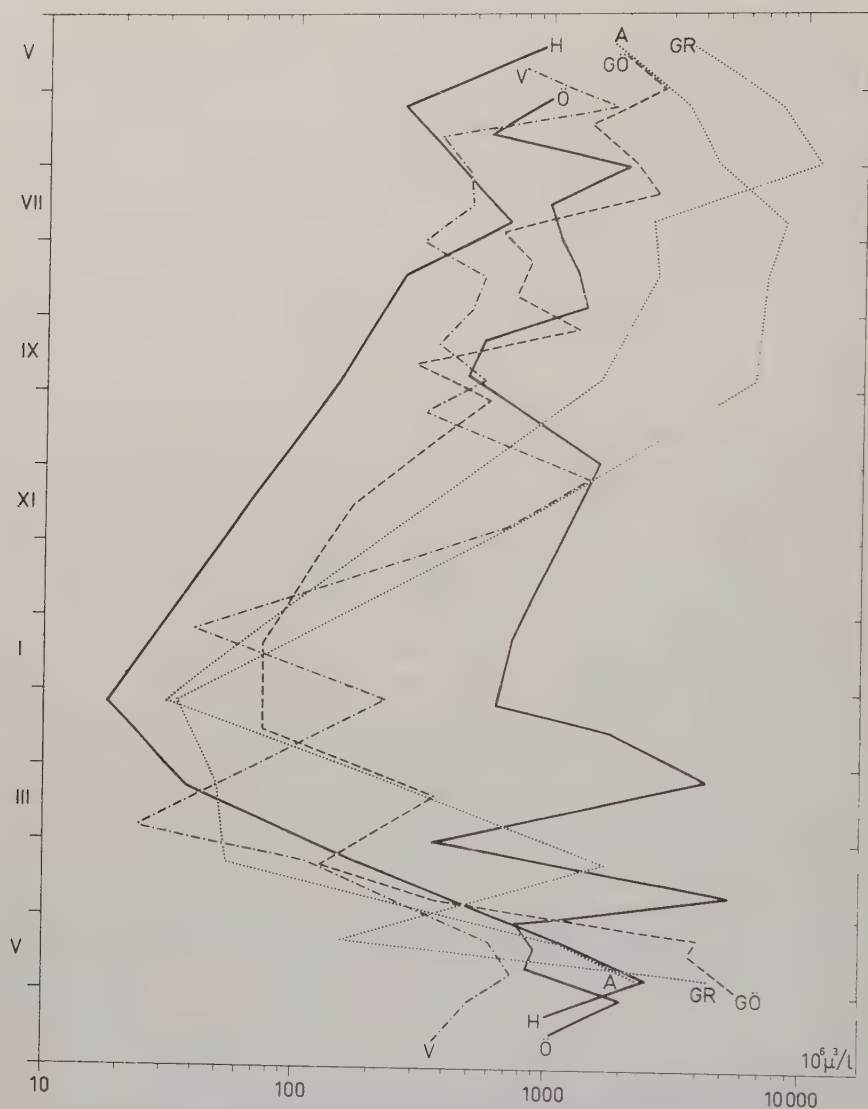


Fig. 3. Seasonal distribution of total phytoplankton volumes at Harö (H), and in Gräsvarpet (GR), Görvälén (GÖ), Andersvedjedjupet (A), Lake S. Vixen (V), and Ösbysjön (Ö).

In the examples above it is mainly diatoms which are the species causing the spring outburst. It was always a very small number of taxa which developed in large quantities. A thorough examination of the samples, however, often gave a long list of species, including many bottom and epiphytic diatoms whirled up by the water circulation. As a rule, all these taxa only occurred in small numbers.

The enormous quantitative development of diatoms, in particular, in connection with the vernal circulation is caused by the increased supply of nutrient substances, but also by change in conditions of light, temperature (see FINDE-NEGG 1943, p. 389; RODHE 1948, p. 123 ff.), oxygen concentration etc. The total volumes of diatoms and the silica concentration in the water of Görväln were shown to be correlated in WILLÉN I, Fig. 11, p. 269. After the spring outburst in 1955 a marked decrease of the silica concentration was recorded. The diagram for Ösbysjön (WILLÉN II, Fig. 11, p. 58) shows no corresponding relation: the diatoms were insignificant in this lake.

Cold water organisms (e. g. *Bicosoeca*, *Chlamydomonas*, *Chlorogonium*, *Glenodinium* and *Stelexomonas*) occurring in the ice-covered lake persisted for a short period after the ice has disappeared. In spring, on the other hand, many organisms which require relatively warm water for their development appear (*Anabaena*, *Aphanizomenon*, *Pediastrum*, *Scenedesmus*, *Tetraëdron*, *Ceratium* etc.) Such an early development was observed in Gräsvarpet and Andersvedjedjupet. In these shallow lakes relatively high water temperatures were recorded during May and June.

In Ösbysjön the predominance of bacteriophytes, euglenophytes and pyrophytes in winter was broken with the change to open water. Some of these organisms certainly occurred during a short transitional period but in general there was a definite change between populations adapted to low oxygen conditions, "mud organisms" (WILLÉN III, p. 217), and those preferring normal oxygen conditions.

In conclusion it may be said that the transitional period from winter to spring (time of ice melting) is of the greatest importance in the developmental sequence of plankton algae in the lakes even if it is not always characterized by the highest total volumes of phytoplankton recorded.

After the vernal water circulation but before the stable summer stratification there was often a period of decreasing total phytoplankton volumes. This period was characterized by maxima, of short duration, of some chrysophytes: *Erkenia subaequiciliata*, *Dinobryon* spp., *Synura petersenii*, *Uroglena americana* etc., all taxa preferring water temperatures below 15°C.

This developmental phase characterized by a predominance of chrysophytes prevailed during the whole summer in some lakes, e. g. in Utålsviken and Ösbysjön. They are both to be referred to the group named "pond lakes" (WILLÉN III, p. 219). Many taxa in particular belonging to *Chlorophyta*, *Cryptophyceae* and *Peridineae* certainly also occurred in these lakes in summer, but these groups never predominated by volume.

Relatively low volume values were recorded in most lakes in summer. Marked exceptions, however, were the lakes in the flada stage: Gräsvarpet and Andersvedjedjupet (Fig. 3). Some differences existed between these two lakes. In Gräs-

varpet (WILLÉN IV, Fig. 24 a, b, pp. 80, 81) cyanophytes and chlorophytes predominated during June (the freshwater phase). By influxes of brackish water these populations were destroyed and the even development of the plankton algae was disturbed. In Andersvedjedjupet chrysophytes and diatoms predominated during June, cyanophytes and chlorophytes during July, cyanophytes and diatoms during August and September, and very high volume values were recorded during the whole summer. In these lakes the chlorophytes (*Dictyosphaerium*, *Crucigenia*, *Pediastrum*, *Scenedesmus*, *Tetraëdron* etc.) consisted of numerous species and played a relatively important rôle by volume. In other lakes, this group was represented by several taxa, but they occurred always in very small quantities (see e. g., WILLÉN IV, Fig. 44, p. 137).

In Görvälän the cryptomonads predominated during July and were followed during August and September by large populations of cyanophytes (*Anabaena*, *Aphanizomenon*, *Microcystis*) and dinoflagellates (*Ceratium*). In Görvälän it was verified that e. g. *Melosira islandica* ssp. *helvetica* occurred in large quantity in the hypolimnion in summer (see ASTRID CLEVE-EULER 1922, p. 66, RODHE op. c., p. 135). In small and shallow lakes (Utålsviken and Ösbysjön) the genus *Melosira* was without significance. The summer conditions in these lakes are apparently not suitable for its survival. In the epilimnion diatoms, as a rule, were of little importance in summer. Among relatively common species *Asterionella formosa*, *Attheya zachariasii* and *Rhizosolenia longiseta* may be mentioned.

Peak volume values corresponding to those found in spring have not been recorded in autumn in any of the investigated lakes. However, a moderate increase of the total volumes was recorded from most lakes and was mainly caused by diatoms, e. g. in Görvälän *Stephanodiscus* spp.; in Andersvedjedjupet *Diatoma elongatum*; in Långtögen *Stephanodiscus* spp.; in Utålsviken *Asterionella formosa* and in Lake S. Vixen *Asterionella formosa*, *Melosira granulata*, *Stephanodiscus* spp. and *Tabellaria fenestrata*. In Långtögen and Ösbysjön *Uroglena americana* (and *U. europaea*) occurred in immense quantities at the end of October. The genus *Uroglena* may occur in early summer, as mentioned above, and in late autumn, but also in winter under the ice. During March 1962, *U. americana* was counted as more than 30 million cells/l in Lake Södra Långvattnet, near Göteborg (West Sweden). Otherwise, the algal development in autumn was characterized by successive disappearance of the late summer species: the cyanophytes, eucchlorophytes, desmids and dinoflagellates, etc. It was hardly possible to find any specific autumnal species; some diatoms and chrysophyte species, however, may encounter suitable nutrient, light and temperature conditions for a maximum of short duration.

Some species occurring in late autumn often persisted in the upper levels even after the ice had formed (e. g. *Aphanizomenon flos-aquae* in Görvälän, WILLÉN I,

p. 253). Otherwise, the number of species recorded in winter was very small and the total volume values were low, $20-80 \cdot 10^6 \mu^3/l$ (Fig. 3). From January to March these low volume values were recorded; in April the days become longer, the snow on the ice melts away and because of these changed conditions new and larger populations often developed immediately under the ice.

In general, some specific cold-stenothermal species occurred in all lakes, but always in small quantities: the chrysophytes *Aulomonas purdyi*, *Bicosoeca* spp. (*B. ainikkiae*, *B. cylindrica* etc.), *Chrysolykos planctonicus*, *Stelaxomonas dichotoma* and many colourless flagellates, some *Cryptomonas* spp., *Dinobryon cylindricum* (in particular in Lake S. Vixen), etc. During the winter period cyanophytes, chlorophytes and diatoms were without significance. – A comprehensive survey of plankton algae occurring in winter in Swedish lakes is given by SKUJA (1956, p. 387 ff.).

As mentioned above, a marked increase both in number of species and in total volumes was recorded toward the end of the ice-period. In the levels immediately under the ice the light became sufficient for a stronger development of plankton algae. Among the chlorophytes the genera *Carteria*, *Chlamydomonas* and *Chlorogonium* occurred in most lakes; among the chrysophytes *Anthophysa*, *Chrysococcus*, *Kephyrion*, *Sphaeroeca*, *Volvochrysis* etc.; among the diatoms *Asterionella*, *Melosira* and *Stephanodiscus* (in Görväln); among the dinoflagellates *Amphidinium* and *Gonyaulax* (at Harö), *Glenodinium* and *Gymnodinium* (in most lakes), etc. Some of these species showed their maximum development before the ice disappeared (e. g. *Chlamydomonas* and *Chlorogonium*), but often they reached peak values in connection with the vernal circulation.

From Fig. 3 it is evident that most of the investigated lakes showed a similar developmental sequence; low total volume values in winter followed by a steep ascent in connection with the melting of the ice. One lake (Ösbysjön), however, clearly deviated from all other lakes during the winter period.

In this lake the highest total volume values were recorded in winter; the bacteriophytes played an important rôle by volume, together with chlorophytes and dinoflagellates. The oxygen concentrations became very low in the shallow lake and as a consequence, specific mud and cold water organisms appeared (see, e. g., WILLÉN II: Figs. 3 a–c, pp. 42–44). These have been listed above, p. 182. They developed in large quantity, being adapted to the various temperature and oxygen conditions which prevailed in the lake during the course of the winter. It was also pointed out above that most of these organisms also occurred in Ösbysjön in summer at levels near the bottom, where a marked tendency toward anaerobic conditions prevailed (WILLÉN III, p. 214). However, at the considerably higher water temperatures in summer some species were not

observed, e. g. *Glenodinium pulvisculus*, *Hyalosoris lamprocystoides*, *Pelosphaera rotans*, *Sarcina tetras*, etc.

Vertical distribution

The vertical distribution of phytoplankton was mainly studied in Görvälén, Sandängsfjärden and Ösbysjön. These bodies of water are of quite different size and shape, thus offering variable conditions for plankton distribution.

The vernal water circulation in Görvälén, during which period the plankton algae are normally equally distributed throughout the whole body of water, was restricted to the upper levels in 1956 because of the occurrence of slightly brackish water at deeper levels (Fig. 2). The gradual changes in chemical composition and algal distribution could be studied in detail (WILLÉN I, Fig. 4c, p. 251, etc.). From 8/V to 28/V 1956 the water was brought into circulation down to the level of 20 m and somewhat deeper together with the accompanying large diatom populations; at 45 m, however, very low total volume values were recorded during the whole period. In 1955 the vernal circulation was complete. In summer (July to beginning of October) the algal development was restricted mainly to the trophogenic layer: considerably lower volume values were often recorded at the level of 5 m and always at 10 m. At deeper levels mainly diatoms and colourless flagellates predominated; in addition dead algae and detritus occurred sinking towards the bottom. After the complete autumnal water circulation (in mid-October) very low volume values were recorded in winter and most organisms occurred in the level immediately under the ice.

In Ösbysjön, as a rule, an uniform algal distribution at the different levels was recorded (WILLÉN II, p. 64) owing to the shallowness of the lake (ca. 3.5 m). Deviations were mainly observed in winter with chlorophytes and pyrophytes concentrated immediately under the ice and with bacteriophytes and euglenophytes near the bottom. In general, this distribution was caused by the light conditions and the concentrations of O_2 and H_2S of the water.

Sandängsfjärden (5–6 m deep), studied in spring 1961 (WILLÉN IV, p. 119 ff.), showed a very distinct stratification. Besides the influence of temperature and oxygen conditions, the salinity here played a decisive rôle for the algal distribution. The temperature ranged from 23.6°C (at 0.5 m) to 7.5°C (at 4.5 m; 9/VI 1961); very low concentrations of oxygen characterized, as a rule, the levels below 4 m, and the specific conductivity often ranged from $\kappa_{20} \cdot 10^6 = \text{ca. } 1,600$ (at 0.5 m) to 8,000 (at 5 m). These environmental conditions were accompanied by plankton populations of quite different compositions: freshwater species near the surface in the outflowing freshwater from all the Utål lakes, brackish water species and specific organisms adapted to low oxygen concentrations in the levels near the bottom and, finally, mixed populations on levels between the two mentioned quite different strata.

Characteristics of lakes recently formed by the land uplift

The conditions along the Baltic coast are rather unusual: because of the land uplift new lakes are being formed and the different stages of isolation can be studied. The rate of land uplift is not equal in the area: it varies between zero in Scania (the southernmost province of Sweden) to 100 cm per century in northern Sweden (BERGSTEN 1930, 1954). The historical development of the Baltic area is treated, e. g., by SAURAMO (1958). In Finland conditions correspond to those along the Swedish coast (see, e. g., SEGERSTRÅLE 1949). Coastal lakes have also been studied in other parts of Europe. Investigations of coastal waters include the surveys given by GESSNER (1957, p. 339 ff.) on "Haffe" in northern Germany, by DE BEAUFORT (1954) on Zuiderzee, by CONRAD (1941) on Belgian brackish waters, and by D'ANCONA *et al.* (1954) on the Venetian Lagoon, etc. However, all these coastal waters have been formed in other ways: a land uplift does not occur in recent time in parts of Europe other than Scandinavia.

The physico-chemical conditions of the water of the Baltic are rather constant and the total volumes of phytoplankton are low, as pointed out previously, p. 177. In lakes influenced by intermittent influxes of brackish water, on the other hand, the environmental conditions are changeable throughout the year. In Gräsvarpet and Andersvedjedjupet the relative proportions between the major chemical constituents of the water showed great seasonal differences (WILLÉN IV, p. 28 ff.). The concentrations of Na, Mg, SO_4 and Cl were raised considerably as a result of the influxes; when the freshwater phase prevailed again Ca and HCO_3 became predominant. These alternations between brackish water and freshwater phases characterize the flada stage (WILLÉN IV, p. 18). Though situated at a very low level allowing similar changes between brackish water and freshwater, Lake Mälaren (Görvåln) does not belong to the same group of lakes: it is a large lake and its connections with the Baltic are regulated by locks. As pointed out above, the sporadic influxes of brackish water which mainly settle in the deeper fjärds disturb the normal water circulation there. They exert a stimulating effect on the development of some planktic algae, especially the diatoms.

In lakes of this area situated ca. 1 m above sea level (Långtögen, Utålsviken) the chemical composition of the water is stabilized, and no specific features indicate that these lakes have been connected with the Baltic only 100–200 years ago. No such influence at all can be expected in lakes situated at higher levels (7–15 m): Ösbysjön, Fräkensjön, Grytsjön, Ramsjön, Tomtsjön (physico-chemical data from the four latter lakes are included in WILLÉN IV, p. 130 ff.). In all these lakes the concentrations of Na and Cl are low, while Ca and HCO_3 are predominant. Even if the absolute values of the different constituents show a considerable amplitude in the mentioned lakes, their relative proportions are

rather constant and closely correspond to the "standard curve" or "Uppland 1-21" (RODHE 1949, p. 378).

As a rule, the specific conductivity ($\kappa_{20} \cdot 10^6$) of natural lowland lake waters in Sweden shows lower values with increasing height of the lakes above sea level, a condition discussed, *i. al.*, by LYSÉN (1960, p. 30 ff.), PUKE (1949, p. 83) and WILLÉN (1954, p. 51). It is not only the height above sea level (the age of the lake) which is the decisive factor; the distance from the coast and hence the influence of small windborn amounts of NaCl especially is also of importance.

With regard to the phytoplankton, lakes situated at very low levels also show some deviating features both of species composition and total volumes.

In connection with the influxes of brackish water some species are brought into the lakes belonging to the flada stage but at the same time most of the freshwater organisms living in these lakes are destroyed. In Fig. 3 the effect of such an influx is shown from Gräsvarpet during July.

In the flada the environmental conditions favour the development of very large populations especially in spring and summer. Many cyanophyte, chlorophyte, chrysophyte and diatom genera here develop in enormous quantities. The position of the lake then determines the duration of these large populations: in Gräsvarpet they get destroyed by several influxes every year; in Andersvedjedjupet the influxes are more sporadic and have less effect.

Among taxa especially common in the flada area the following may be mentioned. *Anabaena* and *Aphanizomenon*, as well as the very thin trichomes of *Oscillatoria limnetica* and *Pseudanabaena catenata*, belonged to the most frequently occurring cyanophytes. *Crucigenia*, *Lagerheimia*, *Pediastrum*, *Scenedesmus* and *Tetraëdron* were all represented by several species. Among the chrysophytes *Dinobryon*, *Synura*, *Erkenia* and some other small flagellates were very common as well as some diatom taxa, among which *Melosira* spp. and in particular *Diatoma elongatum* were most frequent and occurred in very large quantities.

However, among the investigated lakes it was only those situated at very low levels above the sea in which both number of species and total volume values were extremely high (WILLÉN IV, Fig. 46, p. 139). As pointed out above, Görvälén may be regarded as an exception. Already at a height of ca. 1 m above sea level not only have the physico-chemical conditions stabilized but also the developmental sequence of the phytoplankton algae. No specific brackish water organisms occurred and, as a rule, the high total phytoplankton volumes, characterizing the flada stage in summer, were not recorded.

A large number of different types of genuine freshwater lakes have been formed, characterized by different ionic compositions and, in consequence, different algal compositions and developmental sequences. Rock composition, quaternary deposits, different kinds of human influence: pollution, regulating

operations, etc. are some factors affecting and determining the development of the lake. Among all types of lakes also occurring at relatively low levels only a few examples have been given in the present paper. Långtögen may be characterized as a moderately eutrophic lake; Utålsviken and Ösbysjön are both small and shallow lakes in a rather advanced stage of senescence, "pond lakes".

Total volume values from Lake S. Vixen (WILLÉN 1961) are also shown in Fig. 3. They have been added as an example of the conditions in a lake situated relatively high above sea level (215 m) and containing transparent, unpolluted water of rather low specific conductivity ($\kappa_{20} \cdot 10^6 = \text{ca. } 70$). Accentuated peaks of the standing crop were caused by diatoms in spring and autumn; some chrysophyte genera were also of some significance. In general, the same seasonal developmental sequence was recorded in this lake as that recorded in most low-lying lakes. The values of the standing crop, however, were considerably lower in Lake S. Vixen.

Environmental conditions and phytoplankton composition in Swedish mountain lakes (from 300 m to over 1,000 m above sea level) have been studied by QUENNERSTEDT (1955), THOMASSON (1951, etc.) and others. A general survey is given by TEILING (1955, p. 212 ff.).

Additional remarks

Importance of nanoplankton

The importance of nanoplankton was early pointed out by HENSEN (1887, pp. 14, 92–93), using "Mikromembranfilter" to sample the small algae. LOHMANN (1908, 1911) performed intensive studies of the composition of nanoplankton and its proportions in relation to net plankton. As pointed out above (p. 176), the division line between net plankton and nanoplankton in practice is vague: even long filamentous algae (*Melosira*, etc.) and single cells of colonial algae (*Asterionella*, *Tabellaria*, etc.) may easily pass through the Müller net.

Comparisons between the distribution of net plankton and nanoplankton have been performed on material from Görväln (WILLÉN I, Fig. 13, p. 271) and Ösbysjön (WILLÉN II, Fig. 19, p. 67). In Görväln the large diatom populations in spring caused high values of the net plankton volumes; corresponding conditions prevailed in Ösbysjön in summer, where *Dinobryon*, *Ceratium* and *Peridinium* spp. were most abundant. Otherwise, there was a definite predominance of nanoplankton in the lakes, not only with regard to number of occurring taxa but also to their total volume values.

In Ösbysjön the major part of the sulphur bacteria present in winter were

included among the nannoplanktic species. Beside the bacteriophytes the following taxa provide examples of nannoplanktic organisms occurring in large quantities in most lakes: *Merismopedia minima*, *Chlamydomonas* spp., *Chlorella* spp., *Crucigenia* spp., *Selenastrum capricornutum*, *S. minutum*, *Chromulina* spp., *Chrysococcus* spp., *Erkenia subaequiciliata*, *Monochrysis* spp., *Ochromonas* spp., *Cyclotella* and *Stephanodiscus* spp. (especially *S. hantzschii* var. *pusillus*), *Rhodomonas* and *Cryptomonas* spp.

RODHE (1958 a, p. 121 ff.; 1958 b, p. 125, etc.) has emphasized the importance of nannoplankton and its rôle in the primary production: "the smaller algae, in general, are more effective producers of organic matter per unit volume than the netplankters are" (RODHE 1958 b, p. 125). In these papers the total volume values from Görväln are included and related to primary production measured by the C^{14} method. – RODHE (1962, p. 28) has also pointed out that nannoplankton plays the principal rôle in the standing crop in high mountain lakes.

When examining samples fixed in Lugol-Rodhe solution it soon becomes evident that beside a number of very common nannoplanktic taxa in each sample, there is also often a moderate occurrence of other small taxa, some of which previously have been regarded as being rare. The distribution of some of these species is discussed in WILLÉN (1962), in which paper some taxonomic notes are given.

It is principally some small chrysophytes of delicate structure which have been studied. Among species of the genus *Dinobryon*, the complex *D. acuminatum* Ruttner – *D. elegantissimum* Bourr. – *D. crenulatum* W. et G. S. West was common, especially in lakes of pond character, Utålsviken and Ösbysjön. *D. petiolatum* Willén belongs to the section *Dinobryopsis*; the species is characterized by a smooth lorica with a long spine (40–60 μ). It was only observed in the brackish water area of the Utål Lake Chain. *Bitrichia chodati* (Reverdin) Chod. is apparently most common in oligotrophic waters (Lake S. Vixen), but it was also observed in samples from Görväln. *Chrysolykos planctonicus* Mack was not uncommon in the Utål Lake Chain and in Ösbysjön. Its development was studied in detail in spring 1961 (WILLÉN IV, p. 102 ff.). However, *B. skujai* (Nauwerck) Skuja (syn. *Chrysolykos skujai* (Nauwerck) Juris), another small species of peculiar shape, was never seen in the investigated lakes but belongs to the cold-stenothermal species common in transparent and oligotrophic waters.

Several species of *Bicosoeca* were observed, mainly in samples from winter and early spring. Cyst development of *B. cylindrica* (Lackey) Bourr. was studied in samples from Lake Erken, Sandängsfjärden and Ösbysjön. *Aulomonas purdyi* Lackey and *Stellexomonas dichotoma* Lackey also belong to the "winter organisms", which have not been studied previously to any great extent.

The two last mentioned species and *Bicosoeca ainikkiae* were used as indicator organisms in an investigation performed in Granfjärden, February to March, 1958 (WILLÉN 1960, p. 136 ff.).

The Granfjärden experiment

Granfjärden is another fjärd of Lake Mälaren and is situated S.W. of the town of Västerås. In winter 1957–1958 an experiment was performed to keep the passage to Västerås free from ice, in order to allow navigation throughout the year. Compressed air was continuously bubbled through a perforated plastic tube lying on the bottom (ca. 22 m deep). The small air bubbles circulated the water and a narrow channel over the plastic tube was kept free from ice. In connection with the experiment phytoplankton analyses were also performed. Samples were collected 6 m, 30 m and 400 m from the “bubble centre” and from different depths. The results of the quantitative analyses are shown in Table 1 and Fig. 4.

On 22/II 1958 the experiment had begun, and very unstable conditions prevailed. Near the bubble centre diatoms (small *Synedra* spp., *Stephanodiscus* spp., etc.) and small flagellates predominated at 1 m and 5 m. 400 m from the centre very low total volume values were recorded with a predominance of small colourless flagellates, a condition normal for the season.

About a month later (25/III 1958), there was a similar composition of the phytoplankton 6 m and 30 m from the centre and at all levels (Fig. 4), with small flagellates predominating; the whole body of water was in circulation. 400 m from the centre, however, there was an undisturbed stratification and here some “early spring algae” had developed at 1 m: *Eudorina elegans*, *Chrysococcus minutus*, *Mallomonas akrokomos*, *Cryptomonas* spp., *Rhodomonas* spp., *Gymnodinium* spp., etc. At 5 m and at deeper levels very low volume values were obtained.

The numbers given in Table 1 are based on complete analyses of the samples. A marked influence of the air bubbling, *i. e.*, complete water circulation, was recorded even 30 m from the centre, while no influence could be observed at 400 m. As mentioned above, it would have been possible to follow the changes of the normal water stratification by counting only some small and charac-

Table 1. Total volumes ($10^6\mu^3/l$) of phytoplankton, Granfjärden, 1958.

Distance from “bubble centre”	22/II			25/III		
	6 m	30 m	400 m	6 m	30 m	400 m
Ice, cm	0	38	43	0	46	60
Level, m						
1.....	58	59	35	18	22	174
5.....	151	33	15	18	20	21
10.....	13	26	17	24	21	18
15.....	11	20	23	27	19	19
22.....	7	19	—	13	17	12

GRANFJÄRDEN

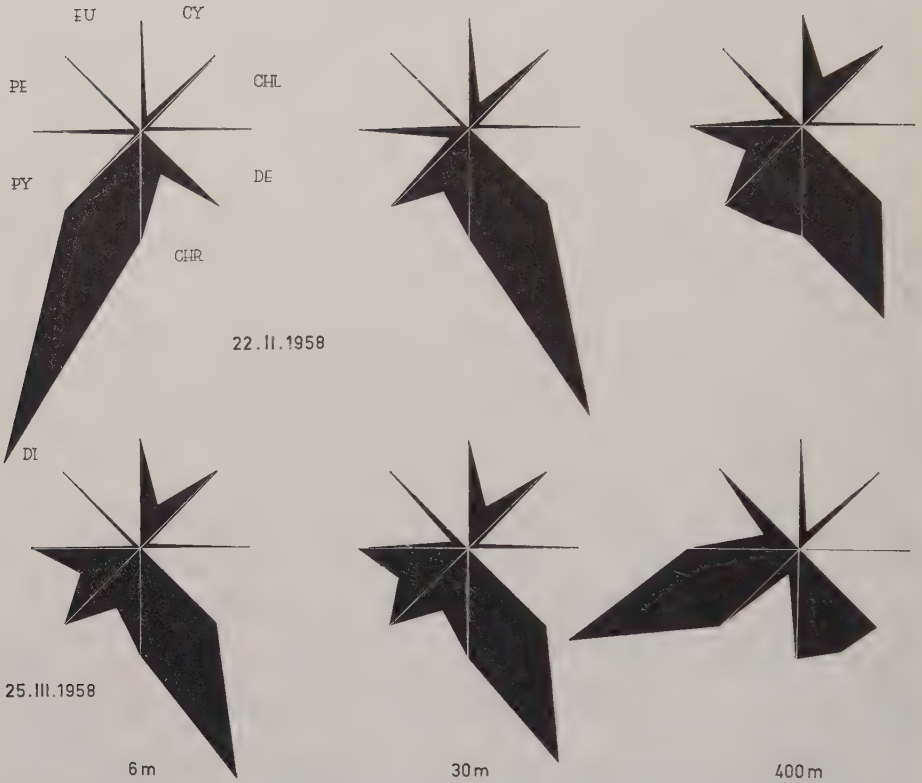


Fig. 4. Percentage distribution of major algal groups, Granfjärden, 1958, at 1.0 m. For abbreviations, see p. 177.

teristic flagellates: *Aulomonas*, *Bicosoeca* and *Stelexomonas*. They showed a similar distribution at all levels in the area close to the bubble centre; *Bicosoeca ainikkiae* was counted as ca. 2,000 cells/l. At the station 400 m from the centre, however, they were most common immediately under the ice like all other taxa.

Summary

In the present paper some comparative qualitative and quantitative phytoplankton investigations of brackish water and lakes situated at low levels near the coast of the Baltic Sea are summarized. The lakes (from sea level up to ca. 7 m) have recently been isolated from brackish water fjärds by the postglacial land uplift.

The quantitative investigations were performed according to the Utermöhl technique; the volumetric determinations were made using the "calculated volume" method.

Differences in the qualitative composition of phytoplankton mainly occurred between the brackish water area and the genuine freshwater lakes. Among the latter, lakes of pond character (Utålsviken and Ösbysjön) showed deviating features in the predominance of chrysophytes. The lakes belonging to the flada stage, *viz.* small lakes in connection with the Baltic and receiving sporadic influxes of brackish water, contained the largest number of species; some specific organisms were also stimulated to an enormous development in this area.

The change from ice covered lake to open water is the critical time in the succession and development of phytoplankton. During the vernal water circulation after the breaking up of the ice more suitable temperature, light, oxygen and nutrient conditions occur and an increase in the standing crops was recorded in all investigated lakes with only one exception, *viz.* in Ösbysjön, where very large populations of bacteriophytes, euglenophytes, pyrrophytes, etc., occurred in winter. However, the highest total volumes of phytoplankton throughout the year were not always recorded in connection with the spring outburst. The flada stage was characterized by very high total volumes of phytoplankton (Fig. 3), in particular in spring and summer, in addition to the largest number of species.

Studies of the vertical distribution of the phytoplankton revealed characteristic features of the lakes. In Görväln (ca. 53 m deep) the normal vernal water circulation and consequently the distribution of plankton was disturbed by a small influx of brackish water (1955–1956); in Ösbysjön (3.5 m deep) specific mud organisms appeared in winter and during a short period in summer, when very low oxygen concentrations occurred (1957–1958). In Sandängsfjärden (5–6 m deep) three zones with very different temperature and salinity conditions as well as phytoplankton composition could be distinguished.

A moderate increase in the total volumes of phytoplankton (caused by diatoms) was often recorded in autumn. In winter low values were obtained in all lakes except in Ösbysjön. Specific "cold water organisms" could be distinguished in all lakes.

Because of the land uplift new lakes are formed continuously along the coast of the Baltic. The flada stage is mainly characterized by specific diatom bottom algae, large phytoplankton populations but a disharmonic developmental sequence during the year. All features characterizing this stage are apparently absent in lakes at a height of ca. 1 m above sea level: both physico-chemical conditions and the developmental sequence of phytoplankton algae are stabilized. Then several different types of lakes may be distinguished: Ösbysjön,

presented in WILLÉN II and III, is an example of a "pond lake"; some remarks are also given about Lake S. Vixen (S. Sweden; 215 m above sea level), where relatively low total volume values were recorded but the same developmental sequence occurred as that in the more low-lying lakes.

Some additional remarks are given about the importance of the nanoplankton in the standing crop, some little known phytoplankton algae, and some indicator organisms used in a study of the phytoplankton development in Granfjärden, Lake Mälaren, where an experiment was performed in the winter of 1958 to keep the passage to the town of Västerås free from ice.

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